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DENSITY-DEPENDENT PRODUCTIVITY DEPRESSION IN PYRENEAN BEARDED VULTURES: IMPLICATIONS FOR CONSERVATION

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Abstract. The main objective of many conservation programs is to increase population size by improving a species' survival and reproduction. However, density dependence of demographic parameters may confound this approach. In this study we used a 25-year data set on Bearded Vultures (*Gypaetus barbatus*) in Spain to evaluate the consequences of population growth on reproductive performance. Unlike its coefficient of variation (CV), mean annual productivity decreased with increasing population size. After controlling for territorial heterogeneity, productivity also was negatively related to the distance to the nearest conspecific breeding pair and to supplementary feeding points where floaters congregate. These results suggest that vulture populations are regulated as posited by the site-dependency hypothesis: as the population increases, average productivity decreases because progressively poorer territories are used. The combined effects of the shrinkage of territories and the presence of floaters around supplementary feeding points seem to be the main causes of productivity decline and are therefore the main determinants of territory quality. This has conservation implications, especially concerning the role of supplementary feeding points. Supplementary feeding should be reviewed given that its usefulness in reducing preadult mortality has not yet been proved and its effect on productivity, as our results suggest, is negative.

Key words: conservation plan effectiveness; crowding mechanisms; density dependence; Gypaetus barbatus; *habitat heterogeneity; Pyrenean Bearded Vulture; site-dependent population regulation; supplementary feeding point.*

INTRODUCTION

The 1979 Birds Directive, which was the first major European Union (EU) law addressing nature conservation on a European scale, is still the main legal framework for the protection of European birds. Although it provides protection for all wild birds, the Directive also requires member states to put into practice special conservation measures for the most threatened species. To help achieve the objectives of the Birds Directive, EU funds dedicated to projects for the conservation of birds and their habitats have been made available since 1992 through the LIFE Nature programs. These co-funded projects (EU and local governments), primarily aimed at strengthening populations, consist of a mixture of different type of actions, mainly oriented toward improving specific demographic parameters such as productivity and survival. The feedback of such actions on population size is rarely investigated.

The Bearded Vulture *Gypaetus barbatus* (see Plate 1) is a large, territorial bird whose numbers and breeding range have declined throughout Europe to the point that LIFE Nature funding is warranted. In Spain, where the bulk of the European population is located, the species reached its lowest levels in the 1970s, when fewer than 40 occupied breeding territories remained in the Pyrenees. After a period of stability up to 1987, the nationwide prohibition of hunting birds of prey implemented at the end of the 1970s and the application of many management actions as part of a Recovery Plan began to take effect. The population of this vulture increased and >90 breeding pairs were located in 2002 (Fig. 1a; Heredia and Margalida 2002). However, this increase in the number of breeding territories only occurred within a restricted geographical range, suggesting that density-dependent changes in demographic parameters were regulating the population (Donázar et al. 2005).

Two different hypotheses relate density-dependent changes in demographic parameters to population regulation in territorial species. The interference hypothesis suggests that reductions in fecundity and/or survival coinciding with an increase in population size are caused by a homogeneous reduction in the quality of available resources due to an increase in agonistic encounters between individuals (Dhondt and Schillemans 1983, Sillett et al. 2004). The habitat heterogeneity hypothesis, however, suggests that the progressive occupation of low-quality territories as density increases causes a decline in the average per capita productivity and/or survival of a population even while its variation

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PLATE 1. Bearded Vulture (*Gypaetus barbatus*) with prey. Photo credit: A. Margalida.

increases, leading to density-dependent regulation (Rodenhouse et al. 1997, Krüger and Lindström 2001, Sergio and Newton 2003, Kokko et al. 2004). Here, dominant or early-arriving individuals occupy high-quality areas and, by means of territorial behavior, relegate subordinate or late-arriving individuals to inferior territories or, when these places are also occupied, to a nonbreeding lifestyle (Newton 1998). This preemptive settlement pattern, coupled with habitat heterogeneity and density-dependent changes in demography, has been defined as site-dependent population regulation (Rodenhouse et al. 1997). This mechanism, which complements and, in certain kinds of species, may even preclude local crowding mechanisms, can generate negative feedback at all population sizes, sometimes independently of local population densities (Rodenhouse et al. 1997).

The behavior of floaters may also be a potential regulatory factor (López-Sepulcre and Kokko 2005). These "surplus" individuals that form a buffer against population fluctuations may harm breeding performance through intraspecific conflicts. The establishment of supplementary feeding points within the distribution area of the breeding population has been the most significant management action in terms of time and effort undertaken to help the Bearded Vulture in the Spanish Pyrenees. The first feeding station was opened in 1983 and, although its importance in the population dynamics of the species remains to be seen, its potential role in reducing preadult mortality (Antor 2001; but see Brown 1997) justified the widespread installation from 1988 to 2002 of 25 additional supplementary feeding points (>15 000 kg/years) between breeding territories. However, the most obvious consequence of increasing food supply was that >80% of nonbreeding birds remained within the breeding territories of other birds during most of the reproductive season (Sesé et al. 2005), unlike the situation in other populations without this intense food supply management (e.g., Brown 1997, Xirouchakis and Nikolakakis 2002). From November to May, at times more than 80 nonbreeding Bearded Vultures can be seen feeding together at some of these points located near breeding territories (R. Heredia, *unpublished data*). This spatial and temporal overlap between the breeding and nonbreeding population fractions may affect the fitness of territorial birds by increasing intraspecific interactions.

In this study we took advantage of 25 years of monitoring of the entire Spanish Bearded Vulture population to evaluate the demographic consequences of the geographical confinement of its population (both the breeding and the nonbreeding part). First, given that Bearded Vultures are cliff-nesting raptors with large territories around nest sites (see review in Margalida et al. [2005]), we tested predictions derived from site-dependent population regulation (Sergio and Newton 2003). We predicted that increases in population size (i.e., the number of breeding territories) should be accompanied by (1) a decline in mean per capita productivity of the population and (2) an increase in the coefficient of variation that would imply the appearance of territories of lower quality (habitat heterogeneity). Therefore, (3) the quality of new territories should be lower than that of traditional

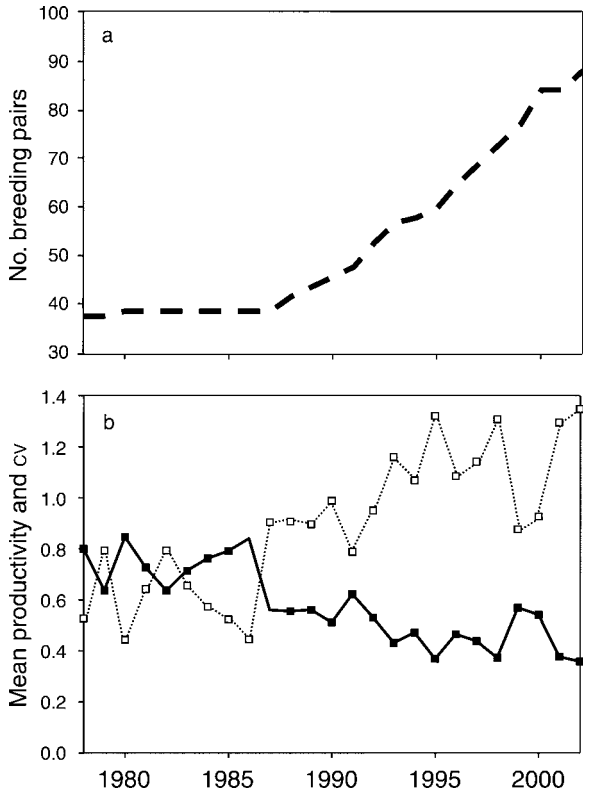

FIG. 1. Changes in (a) number of breeding pairs of Bearded Vultures (*Gypaetus barbatus*) in the Spanish Pyrenees and (b) mean productivity (solid line and black points) and its coefficient of variation (dashed line and white points) during the study period (1978–2002). Productivity is defined as the number of fledglings produced per territorial pair.

territories. However, if increases in the number of breeding pairs have promoted a packing process, interference between neighboring pairs may complementarily affect reproductive parameters. Thus, (4) proximity to other breeding territories (measured as distance to nearest neighboring pair), should also decrease the productivity of territories by (5) reducing the quality of all territories in the population. Because intraspecific interference could also be caused by the coexistence of breeding and nonbreeding birds, (6) territories located near supplementary feeding points (where floaters are congregated) should be less productive than territories located farther away. Moreover, because intraspecific interactions (interference) should be more frequent in territories located in high-density breeding areas and near supplementary feeding points, (7) productivity should be lower at these sites.

METHODS

Census, territories, and reproductive data

The whole Bearded Vulture population in the Spanish Pyrenees (2100 km^2) was monitored from 1978 to 2002. All territories known to have been occupied by the species and potential breeding areas were searched during the breeding season (i.e., pre-laying, incubation, and nestling periods, from early November to August). Each year, the study area was carefully searched for birds, their nests, or other signs of occupancy (e.g., territorial behavior). Occupied territories were located on the basis of territorial and/or courtship activity and then repeated visits were conducted to record breeding parameters (see Margalida et al. 2003). A maximum of one nestling is reared per breeding attempt. Productivity was measured as the average number of fledglings raised per territorial pair, including breeding failures.

Territories occupied since 1978 were considered as *traditional sites*; in a scenario of habitat heterogeneity and ideal despotic distribution, these sites should correspond to the best quality areas. Territories colonized during the period of population increase were classified as *new territories*.

Explanatory variables

Intraspecific relationships.—Inter-year changes in population breeding density were measured as changes in the numbers of territorial pairs within the study area. Local breeding densities were measured annually at a finer scale, using the distance to the nearest neighboring conspecific pair. This index, commonly used as a measure of territoriality in raptors (e.g., Carrete et al. 2006), may account for both food exploitation and agonistic intraspecific interactions between neighbors. Moreover, it has proved to be a good estimator of intraspecific relationships for Bearded Vultures (Donázar et al. 1993).

Other Bearded Vultures congregate at supplementary feeding points (mainly nonterritorial birds; R. Heredia, *unpublished data*) and may interact with territory owners (Bertran and Margalida 1996, Margalida and Bertran 2005). Large and small feeding points differ in the number of birds that they attract (R. Heredia, *unpublished data*). Large supplementary feeding points ($n = 5$) are artificially provided with >5000 kg of lamb legs each year, and as many as 80 birds may congregate there during early spring (R. Heredia, *unpublished data*). On the other hand, small supplementary feeding points ($n = 21$) may see only ~6–12 birds together because the food supply is intermittent and less abundant (<3000 kg of legs of lambs at year; R. Heredia, *unpublished data*). Thus, we calculated the distance from each territory to the nearest large (DLFP) and small (DSFP) supplementary feeding point, and to the nearest supplementary feeding point of any type (DFP) as another surrogate of intraspecific interactions. Because supplementary feeding points, as well as breeding territories, varied from one year to another, variables were measured annually.

Habitat quality.—Donázar et al. (1993) found that the probability (p) of occupation of a cliff by Bearded Vultures in the Spanish Pyrenees could be predicted by the model:

$$\ln[p/(1-p)] = -33.93 + 0.09058(\text{relief}) + 1.644(\text{distance to nearest neighbor}) + 0.009867(\text{altitude}) - 4.024 \times 10^{-6}(\text{altitude})^2 + 0.9451(\text{distance to village}).$$

This model correctly classified 79.3% of nesting cliffs and 76.6% of random points, a classification that is 56% more accurate than random choice ($\kappa = 0.559$, $z = 8.337$, $P < 0.001$).

Using this model, we calculated the probability of occupation of a territory (traditional and new) as an index of territory quality that summarizes both the general features of breeding sites and conspecific presence (Q_{NND}). To separate habitat from conspecific effects, we recalculated by cross validation the probability of cliff occupation, taking into account only relief, altitude, and the distance to the nearest village (Q_{HAB}; for a detailed description on methods used, see Donázar et al. 2005).

Statistical analyses

At the population level, relationships between the number of breeding pairs, average productivity, and its CV were assessed by Spearman rank correlations (Sergio and Newton 2003). At a finer scale, we first explored the existence of habitat heterogeneity through generalized linear mixed models (GLMM; McCullagh and Searle 2000) by testing the effect of territory (as a fixed effect) on productivity while controlling for year (random effect). We used the logistic (0, no chick fledged; 1, one chick fledged) as a link function and the binomial as an error distribution. Because the random term "year" was not significant (see *Results*), we subsequently used generalized linear models (GLM, McCullagh and Nelder 1989) to distinguish factors explaining variance in productivity. To control for the nonindependence of data recorded in the same territory, we included the territory in models as a fixed term ("territory") and not as a random term, because we were monitoring the whole population. Finally, a forward stepwise procedure to assess the relative contribution of each variable resulted in multivariate models in which only significant effects were retained. For each significant model, we calculated the percentage of deviance explained (100 − (model deviance/null model deviance)100). Analyses were done using the SAS package (Littell et al. 1996).

RESULTS

Long-term changes in population size and productivity

From 1978 to 2002 the Bearded Vulture population in the Spanish Pyrenees increased from 38 to 91 breeding pairs (Fig. 1a). During the same period, the mean annual productivity of the population declined from 0.8 to 0.37 young/territorial pair ($r_S = -0.79$, $P < 0.0001$, $n = 25$) and its coefficient of variation increased ($r_S = 0.78$, $P < 0.0001$, $n = 25$). This negative correlation between productivity and its coefficient of variation ($r_S = -0.99$, $P < 0.0001$, $n = 25$; Fig. 1b) suggests that increasing use of poor-quality territories as the population increased caused density dependence. Indeed, when "territory" was included in GLMM as a fixed effect ($F_{65,814} = 2.06$, $P < 0.0001$) while controlling for year effects ($z = 1.52$, $P = 0.0648$), the model explained >25% of deviance in productivity. However, when we split the data set into two groups (i.e., before and after 1988) to repeat models, we found that in both cases "territory" explained a similar percentage of deviance (26.80% and 28.05%, respectively). This may suggest that its importance is the same for both periods, and variability among territories did not increase after population growth. Thus, although our data support the existence of habitat heterogeneity within the breeding population (predictions 1 and 2), other mechanisms also must have been depressing productivity during the period of population growth (post-1988).

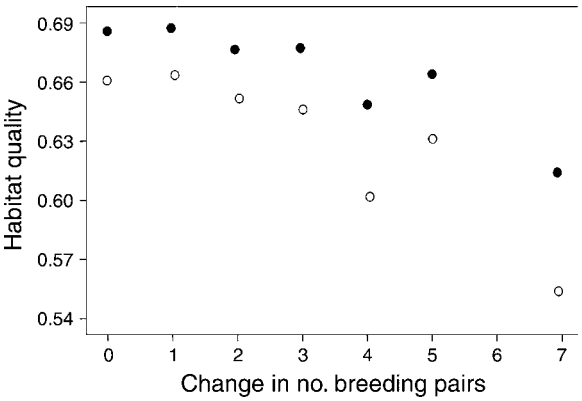

FIG. 2. Relationship between changes in number of breeding pairs of Bearded Vultures in the Spanish Pyrenees and both indexes of habitat quality: Q_{HAB} (habitat variables: relief, altitude, and distance to the nearest village; open dots) and Q_{NND} (habitat variables plus nearest neighbor distance to a breeding conspecific pair; solid dots).

Population size and territory quality

Both indices of territory quality were negatively correlated with changes in the number of breeding pairs (for Q_{NND}, $r_S = -0.76$, $P < 0.0001$, $n = 25$; for Q_{HAB}, $r_S = -0.66$, $P < 0.0001$, $n = 25$), thus supporting prediction 3 and the habitat heterogeneity hypothesis. However, although the habitat quality index obtained by including only territory features (Q_{HAB}) dropped by 13%, the same index including distance to the nearest breeding pair (Q_{NND}) declined by 20%. Thus, although the increase in population resulted in some pairs occupying intrinsically poorer territories (Q_{HAB}), proximity between conspecific breeding pairs (Q_{NND}) seemed to be the most important factor reducing habitat quality and, therefore, productivity (Fig. 2).

Under the habitat heterogeneity hypothesis, productivity in traditional territories (those occupied at least since 1978) should be better and more stable than in new

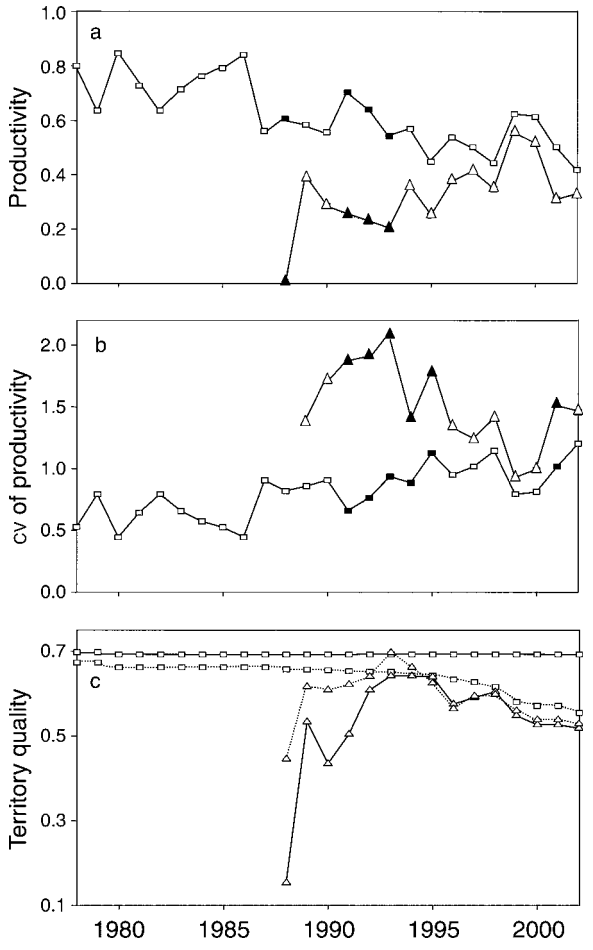

FIG. 3. Changes in (a) annual productivity of Bearded Vultures in the Spanish Pyrenees, (b) coefficient of variation of the productivity, and (c) habitat quality (Q_{HAB}, solid line; Q_{NND}, dashed line) in traditional territories (squares) and new territories (triangles) through the study period (1978–2002). Significant differences in parameters are shown as solid symbols.

ones (those occupied from 1988 onward, when the population started to increase). Although new territories were significantly less productive (Fig. 3a) and more unpredictable (Fig. 3b) initially, from 1988 to 1993, (Mann-Whitney U tests range = 19.5–183; P range = 0.012–0.047), these differences lessened and disappeared altogether in the final years (1994–2002), when territories became more homogeneous in terms of their suitability for reproduction (Mann-Whitney U tests range = 188–753; P range = 0.089–0.401; Fig. 3a, b). Accordingly, we found a significant interaction between type of territory (traditional or new territory) and the distance to the nearest occupied pair in our GLM (NND × type of territory: $F_{1,857} = 4.86$, $P = 0.045$). Thus, although the intrinsic quality (Q_{HAB}) of traditional territories remained constant with time (Fig. 3c), a rise in the number of breeding pairs may increase intraspecific interactions, thereby reducing the other quality index (Q_{NND}).

Interference with conspecifics

The distance to conspecific breeding pairs also reduced productivity (for territory, $\chi^2 = 351.60$, df = 87, $P < 0.0001$; for I_{NND}, $\chi^2 = 3.74$, df = 1, $P = 0.053$, 25.57% of deviance explained). However, potential interference does not seem to affect all territories in the same way, because an interaction between territory and distance to conspecific pairs was significant in models ($\chi^2 = 60.07$, df = 33, $P = 0.003$, 30% of deviance explained by adding the interaction in the model).

Productivity declined with proximity to small supplementary feeding points (for D_{SFP}, $\chi^2 = 31.04$, df = 1, $P < 0.0001$, 2.67% of deviance explained), even when habitat heterogeneity was included in models (for territory, $\chi^2 = 316.32$, df = 87, $P < 0.0001$; for D_{SFP}, $\chi^2 = 31.04$, df = 1, $P < 0.0001$, 29.92% of deviance explained). Distance to large supplementary feeding points had no effect per se on productivity ($\chi^2 = 0.65$, df = 1, $P = 0.42$), although it was significant when heterogeneity among territories was considered (for territory, $\chi^2 = 367.52$, df = 87, $P < 0.0001$; for D_{LFP}, $\chi^2 = 5.18$, df = 87, df = 1, $P = 0.023$, 28.36% of deviance explained). As happens with distance to conspecific breeding pairs, not all territories were affected in the same way. When the interactions between territory and distances to both large and small supplementary feeding points were taken into account, models indicated that some territories might be more affected than others by their proximity to supplementary feeding points (for the interaction of territory and D_{SFP}, $\chi^2 = 114.57$, df = 37, $P < 0.0001$, 40% of deviance explained including the interaction; for the interaction of territory and D_{LFP}, $\chi^2 = 63.12$; df = 63, $P = 0.0047$, 33.16% of deviance explained by the model including the interaction).

Even when all territories are not equally affected, the distances to both the nearest conspecific pair I_{NND} and to the nearest supplementary feeding points (both small D_{SFP} and large D_{LFP}) have a negative effect on productivity. Although there is a certain degree of variability in their responses, territories located near supplementary feeding points that are also near to other Bearded Vultures breeding territories had lower productivity than territories with less conspecific pressure (Table 1, Fig. 4a, b).

DISCUSSION

Ecological framework: territory compression and coexistence between breeders and floaters

Research on population regulation has focused primarily on measuring density dependence, whereas the proximate mechanisms by which density can affect demographic rates are less well understood (Hixon et al. 2002). Here we present evidence to suggest that, in accordance with other studies on territorial raptors (e.g., Krüger and Lindström 2001, Sergio and Newton 2003, Carrete et al. 2006), habitat heterogeneity plays a key role in the population regulation of Bearded Vultures.

TABLE 1. Models relating productivity of breeding Bearded Vulture territories to distance to the nearest conspecific breeding pair (I_{NND}) and the nearest supplementary feeding point (D_{SFP}, small; D_{LFP}, large).

Effect	χ^2	P
Large supplementary feeding (model explains 37% of deviance)		
Territory	348.10	0.0001
I_{NND}	4.15	0.0465
D_{LFP}	4.15	0.0416
Territory × I_{NND}	62.43	0.0015
Territory × D_{LFP}	55.57	0.0327
Territory × I_{NND} × D_{LFP}	10.85	0.0283
Small supplementary feeding (model explains 45% of deviance)		
Territory	325.86	0.0001
I_{NND}	2.64	0.1041
D_{SFP}	1.25	0.2639
Territory × I_{NND}	51.38	0.0217
Territory × D_{SFP}	104.22	0.0008
Territory × I_{NND} × D_{SFP}	38.88	0.0004

Note: In contrast to the text, here we present models including all interactions (×) among variables.

As the Pyrenean Bearded Vultures are not individually marked, we cannot tell whether habitat heterogeneity is a consequence of sites possessing different suitabilities for reproduction or for survival (Breininger and Carter 2003, Lambrechts et al. 2004, Carrete et al. 2006). However, our findings that productivity declined and its variation increased as Bearded Vulture populations increased from 38 to 91 pairs (during 1987–2002) are new and relevant for both basic and applied ecology because they show that population regulation is not simply a result of interference (i.e., ideal free distribution) or preemptive use of space. Moreover, traditional discussions on density dependence in territorial systems are mainly based on data obtained from populations in demographic equilibrium, where crowding mechanisms are usually precluded. Our data, collected throughout a period of population growth, show that when high-density situations are encouraged, demographic density dependence in territorial birds can occur because of the combined effects of site quality (ideal despotic distribution) and crowding mechanisms (ideal free distribution). Moreover, and no less importantly, we also show that nonbreeding birds can make up a significant fraction of the whole population and that their effects on breeding individuals as scramble competitors must be taken into account (López-Sepulcre and Kokko 2005).

Age differences could be proposed as an alternative hypothesis to explain productivity variation between territories (Forslund and Pärt 1995), where inexperienced birds occupying new territories increase their productivity over the years, and senescence promotes a progressive decay of productivity in traditional sites. Although we were not able to test age effect on reproduction (Bearded Vultures are not individually marked), and therefore we cannot discard it, our data show strongly that habitat heterogeneity and interference play a role in productivity depression, explaining an important percentage of deviance.

Density of conspecific competitors has been shown to negatively affect territory size in several bird species (see review in Newton [1998]), independently of food availability (e.g., Arcese and Smith 1988, Stamps 1990). Although we have no information on either home range size or its change with density, our results suggest that this Bearded Vulture population may have suffered a process of territorial compression associated with an increase in the number of breeding pairs (nearly 25% reduction in the mean nearest neighbor distance between 1987 and 2002). This may be affecting the productivity of the population, as has been suggested by Donázar et al. (2005), who found that, after 1991, the

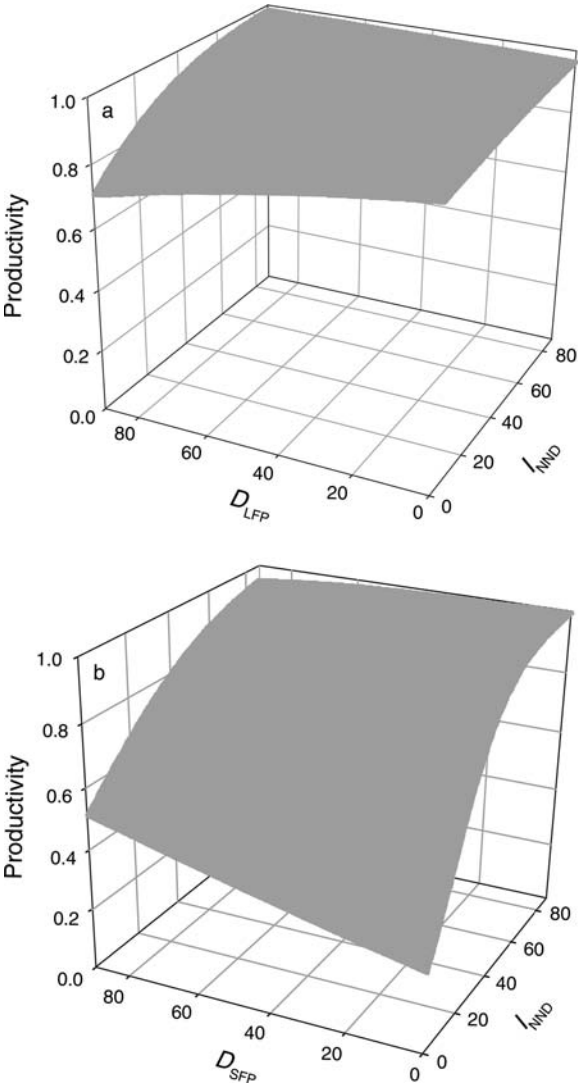

FIG. 4. Interactive effects of distance to the nearest conspecific breeding pair (I_{NND}) and distance to the nearest (a) large (D_{LFP}) and (b) small (D_{SFP}) supplementary feeding point on productivity of Bearded Vultures in the Spanish Pyrenean Mountains.

best-fit model for predicting territory occupation does not include the distance to the nearest occupied Bearded Vulture nest. Moreover, Donázar et al. (1993) did not find any relationship between breeding success and distance to conspecific breeding pairs, suggesting that productivity was not limited by any density-dependent mechanism before 1991. Consequences of territory compression have been explored in other species, where increases in density are accompanied by increases in aggressive behavior among territorial animals and increases in costs associated with territory defense (e.g., Calsbeek and Sinervo 2002, Mougeot et al. 2003, Sillett et al. 2004). In these cases, territory shrinkage and territorial disputes associated with high-density situations affected reproduction and had fitness costs for territorial animals (Gordon 1997, Calsbeek and Sinervo 2002, Ridley et al. 2004), as in our Bearded Vulture population. However, we found that not all territories were equally affected by increases in the number of breeding pairs. Territories located at high-density situations became less productive and more unpredictable than territories located far away from conspecific pairs, indicating that, in the present situation, proximity to other breeding pairs could be the main factor promoting territory quality and also, to some extent, habitat heterogeneity in this closed population.

Proximity to supplementary feeding points where nonbreeding birds congregate was also detrimental for reproduction. For species with delayed maturity, such as many long-lived raptors, spatial segregation between dispersing and breeding birds is a common feature (Newton 1979). This is because preparation for reproduction governs preferences among breeders, whereas food is the main driving force underlying habitat selection patterns in dispersing birds (e.g., Brown 1997, Bustamante et al. 1997, Mañosa et al. 1998, Hirzel et al. 2005). In our study area, however, the high availability of food resources associated with supplementary feeding points allows a high number of nonbreeding Bearded Vultures, which otherwise would be occupying different areas (Brown 1997, Xirouchakis and Nikolakakis 2002, Hirzel et al. 2005), to coexist within the spatial distribution of the breeding population. Contrary to the social behavior observed in other species where floaters and territorial birds may coexist in areas of high food supply (e.g., Blanco and Tella 1999, Forero et al. 2002), Bearded Vultures are territorial birds that defend exclusive breeding areas against both conspecifics and heterospecific birds (e.g., Margalida and Bertran 2000, 2005, Bertran and Margalida 2002). Thus, high concentrations of floaters around breeding territories (as happens near supplementary feeding points) may increase the time being spent in agonistic encounters and, therefore, may reduce breeding success. Moreover, conspecific crowding can be a significant stressor that may alter glucocorticosteroid release, causing both physiological and behavioral changes that may affect population dynamics (Rotllant et al. 1998, Creel 2001, Romero 2004).

Management implications for conservation plans

The establishment of supplementary feeding points for the management of vulture populations has been used during reintroduction programs to maintain birds close to release areas (Griffon Vultures, *Gyps fulvus*, in France; Sarrazin et al. 1996), to increase food supply (Piper et al. 1999), or even as a potential solution to reduce poisoning (California Condor, *Gymnogyps californianus*, in the United States; Meretsky et al. 2000). However, to our knowledge, no rigorous tests of the long-term effects of supplementary feeding on population dynamics have been carried out. Our results suggest that these management actions aimed at increasing the number of breeding pairs within the present distribution of the species and those attracting nonbreeders within the spatial range of the breeding population of Bearded Vultures should be reconsidered. In particular, the strategy of food supplementation should be reviewed because it seems to be one of the main potential factors promoting the congregation of nonbreeding birds around breeders. Decisions to disperse or to remain in the local population are influenced by local intraspecific competition (Clarke et al. 1997, Perrin and Mazalov 1999, Gandon and Michalakis 2001, Lambin et al. 2001, Forero et al. 2002, Serrano et al. 2004). Thus high food availability within the geographical range of the breeding population could be keeping dispersing birds in their natal areas. The expected consequences of reducing food availability would be both an increase in the movements of floaters outside the distribution range of breeding birds, thereby reducing direct interactions in territories located near feeding points, and a geographical expansion of the breeding population to other suitable areas, as is proposed in the Recovery Plan of the species in Spain. Supplementary feeding points were opened on the basis of their importance in increasing juvenile survival (Antor 2001). However, direct evidence of a causal link between food supplementation and juvenile survival is lacking. Juvenile populations may have increased as a result of other factors such as an increase in wild ungulate populations (Razin and Bretagnolle 2003) or the reduction in direct human persecution through legislation since early 1980. Moreover, although predictable food resources would theoretically be advantageous when accidental poisoning was significant, in fact no analyses comparing the survival of the species in the Pyrenees with other areas exist because of the geographical range restriction of the species.

In spite of the large amount of money invested since 1994 via LIFE Nature projects in the conservation of the Bearded Vulture (six LIFE Nature projects costing >6 million euros), the effectiveness of these management actions has rarely been tested. A scientifically rigorous and adaptive approach to wildlife management demands that management actions be conducted within a frame-

work of quantitative predictions, treatment, evaluation, feedback, and response. Conservation involves deciding on appropriate actions from a wide range of options, often in the absence of supporting evidence. Moreover, management decisions are often required urgently when population sizes are severely threatened. However, where more fundamental questions are involved (such as the effects on demographic rates or the viability of a population), decision makers do not usually know which action will work or what the actual effect will be (Pullin et al. 2004). Supplementary feeding points may have been useful at the beginning of the management period, when the Bearded Vulture population was at a lower density and territory establishment was desirable. Although it could be argued that the breeding population of Bearded Vultures in the Pyrenees is "safe," given its increased numbers, the actual risk of extinction today as a consequence of its restricted geographical distribution has not changed. Therefore, conservation actions should be focused on expanding the geographical range of the population to reduce the probability of stochastic catastrophes (Caughley 1994) and to increase the value of demographic parameters. In this sense, experimental management actions such as the supplementary feeding of breeding pairs are currently in practice in some areas and their effectiveness in increasing productivity will have to be evaluated in the near future.

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